Short-term movements of juvenile and neonate sandbar sharks, *Carcharhinus plumbeus*, on their nursery grounds in Delaware Bay

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Synopsis

We investigated short-term movements of neonate and juvenile sandbar sharks, *Carcharhinus plumbeus*, on their nursery grounds in Delaware Bay. The majority of sharks tracked limited their movements to water less than 5 m deep, remained within 5 km of the coastline, and occupied oblong activity spaces along the coast. In addition to site-attached coastal movements observed, several sharks moved entirely across Delaware Bay or spent considerable time in deeper portions of the central bay. Sharks tracked on the New Jersey side of the bay tended to spend more time in deeper water, farther from shore than sharks tracked on the Delaware side. Observation-area curves estimated that optimal tracking time for sandbar sharks in Delaware Bay was 41 h. Indices of site attachment showed that movement patterns of tracked sandbar sharks varied from nomadic to home ranging. There was no significant difference in rate of movement for day/night, crepuscular periods, or between juveniles and neonates. In general, young sandbar sharks patrolled the coast and appeared to be site attached to some extent, but were capable of making longer excursions, including movement entirely across Delaware Bay.

Introduction

The sandbar shark, *Carcharhinus plumbeus*, is a large coastal shark distributed worldwide in temperate and tropical seas. The species is highly migratory and may travel thousands of kilometers every year (Kohler et al. 1998). In the Northwest Atlantic, adult sharks range from Cape Cod, Massachusetts to northern Florida during the summer, then migrate south in late September and early October to warmer, deeper offshore water from the Carolinas to Florida and into the Gulf of Mexico where they spend the winter (Springer 1960, Compagno 1984). Sandbar sharks utilize shallow coastal bays and estuaries along the Mid-Atlantic bight from Great Bay, New Jersey (Merson 1998) to Cape Canaveral, Florida (Springer 1960, Merson & Pratt 2001), and the Gulf of Mexico (Carlson 1999) as

pupping grounds. Pregnant females presumably enter these waters in late spring and early summer, give birth, and depart shortly afterwards. Both neonates (young of the year) and juveniles (ages one and older) occupy the nursery grounds. Neonate sandbar sharks utilize these areas as primary nursery grounds – areas where young of the year live for weeks, months or years after parturition (Bass 1978, Castro 1993). After the neonates have migrated south into the coastal ocean for the winter, they return to their natal grounds as juveniles and remain there for the summer. Thus, these nursery areas also function as secondary nursery grounds, which juveniles occupy before reaching maturity (Bass 1978). Age and growth studies indicate that juveniles return to nursery areas each summer for as many as 7 (Casey et al. 1985) to 16 years (Casey & Natanson 1992, Merson 1998).

Sandbar sharks are one of the most economically important shark species in the southeastern United States shark fishery and are presently considered 'overfished' (NMFS 1999). Understanding space utilization and site fidelity within nursery areas is important for determining spatiotemporal distributions and habitats essential to neonate and juvenile sandbar sharks. Home range traits, such as size, shape and degree of overlap, are also indicators of an animals' feeding strategy and community characteristics (Schoener 1981). In the aquatic environment these traits are influenced by physical factors such as water temperature, salinity, bathymetry, and tidal currents. Home range and site fidelity have been investigated for several shark species: lemon, *Negaprion brevirostris* (Morrissey & Gruber 1993), white, *C. carcharias* (Klimley & Anderson 1996, Goldman & Anderson 1999) gray reef, *C. amblyrhynchos* (McKibben & Nelson 1986), and scalloped hammerhead shark, *Sphyrna lewini* (Klimley & Nelson 1984, Klimley et al. 1988, Holland et al. 1993). However, home range and site fidelity have not been explored for juvenile sandbar sharks during their seasonal occupation of a coastal nursery.

Some information is available on the short-term movements of sandbar sharks in estuarine habitats. Previous sandbar shark tracking studies have revealed general characteristics of short-term behaviors in a nursery area but none have determined home range for these sharks. Medved & Marshall (1983) tracked 20 juvenile sandbar sharks in Chincoteague Bay, Virginia, using floating styrofoam balls attached to the animal with a short line for up to 9 h, and tracked three with acoustic pingers for 10 h. The sharks occupied a range of water depths, from tidal flats to relatively deeper channels. Direction and rate of movement were approximately equal to those of the tidal current, and straightness of movement was observed more often during periods of high current speed. More recently, 10 juvenile sandbar sharks were tracked in Chesapeake Bay for up to 50 h with pressure sensitive transmitters (Grubbs 2001). These sandbar sharks appeared to be at least 3 m from the bottom 50% of the tracking time and activity space was as much as 275 km^2, centered over deep channels in the lower portion of the bay. Track direction and current heading were highly correlated.

The objective of the present study was to describe neonate and juvenile sandbar shark movements during their summer occupation of Delaware Bay. The investigation was aimed at elucidating daily movement patterns, determining the presence of a home range by using site attachment indices, and investigating site specificity among individuals tracked using acoustic telemetry.

Methodology

Neonate and juvenile sandbar sharks were tracked in Delaware Bay during the summers of 1998 and 1999. Generally, tracking studies commenced in late June or early July of both years, when newborn sharks appeared in the bay, and juveniles returned to the bay after their winter migration. Subsequent tracks were made during the months of July, August and September when sandbar sharks continued to reside in the bay.

Study site

Delaware Bay is a large, well-mixed estuary (Figure 1). The area where sandbar sharks were caught and tracked was bounded by the bay mouth between Cape May, New Jersey and Cape Henlopen, Delaware north to the 39°10′ parallel. Total area of the bay is approximately 2000 km^2, averaging 24 km across and is 45 km at its widest. The bay is shallow, averaging 6.3 m depth with extensive shoals along the New Jersey and Delaware coasts (Kraft 1991). Currents are tidally dominated and turbidity is high (Sharp 1991). Bottom substrate throughout most of the bay is fine-grained muddy sand (Weil 1977). The water chemistry in the lower bay is homogeneous (Michels 1996), and salinity and temperature are relatively constant throughout the lower bay at any given time during the nursery season. Water temperatures range from 15°C in late spring to 29°C in late summer, and salinity from 23‰ to 30‰ (Merson 1998).

Tagging

Juvenile and neonate sandbar sharks were caught on rod and reel or 50 gangion long line with 12/0 Mustad hooks with a depressed barb. The longline was set for 30 min in locations where Merson & Pratt (2001) had found aggregations of young sharks in previous years. Upon capture, sharks were measured to the nearest centimeter total length (TL) and weighed with a spring scale to the nearest 0.1 kg. A blue identification tag (Rototag) from The National Marine Fisheries Service Cooperative Shark Tagging Program (Kohler et al.
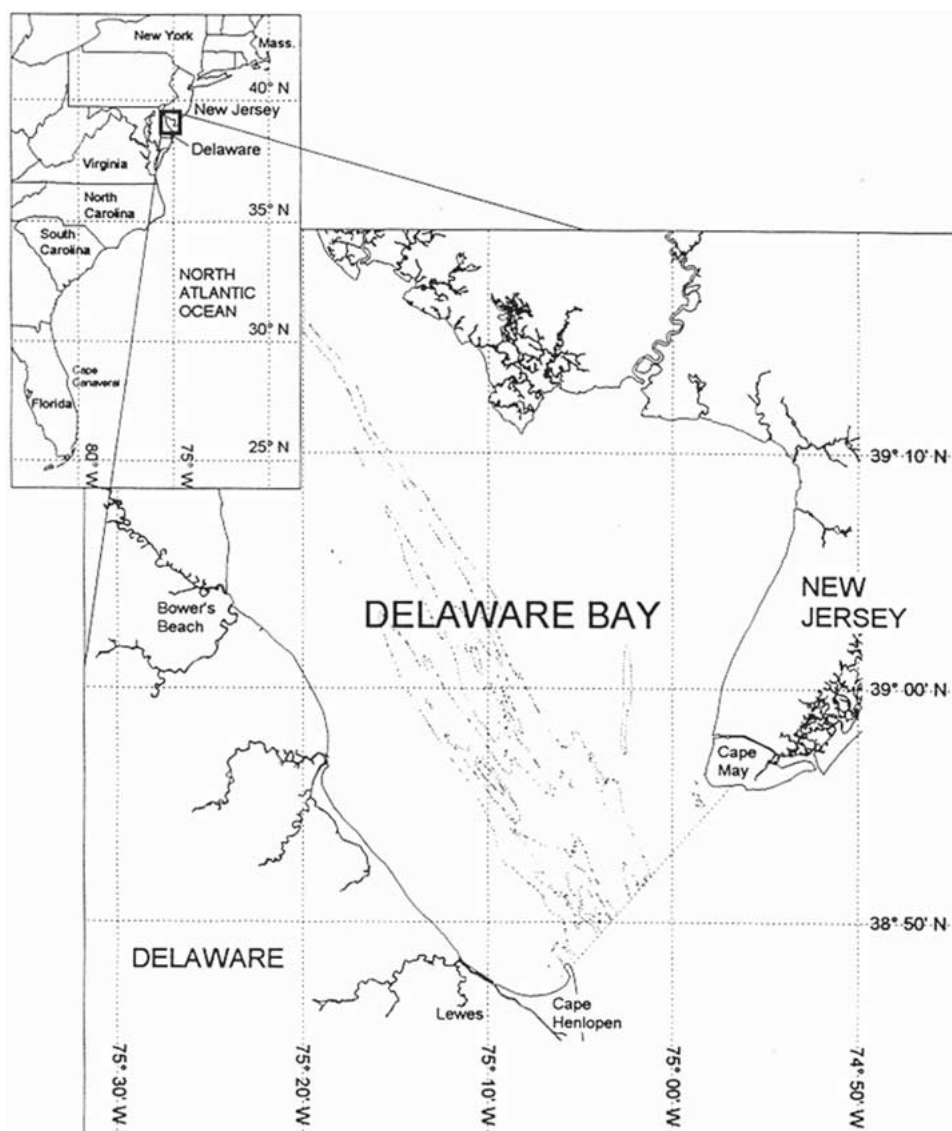
Figure 1. Map of the United States East Coast with enlarged area showing the Delaware Bay study area where sandbar sharks were tracked during summer 1998 and 1999.

1998) was applied to the first dorsal fin. An acoustic transmitter was then attached to the Rototag with galvanized steel wire such that the transmitter trailed behind the first dorsal fin of the shark as it swam. A field test showed that the wire corroded in the surrounding seawater in approximately 30 days, thereby detaching the transmitter from the Rototag, and the shark. Only sharks appearing to be in excellent condition were tracked.

Telemetry

Telemetry equipment consisted of acoustic transmitters, a VR60 receiver, a V10 directional hydrophone, and VSCAN tracking software (Vemco Ltd., Nova Scotia). Transmitters were individually coded by the manufacturer at different frequencies (60–76.8 kHz) and pulse periods (1.0–1.5 s) to differentiate between tagged individuals. Three types of transmitters were

used for this study, the choice of which depended on the size of the shark. Neonate sharks were fitted with V8 transmitters (8 mm diameter, 36 mm length, 3.5 g in water), whereas juveniles received V16 transmitters (16 mm diameter, 59 mm length, 11 g in water). One juvenile was fitted with a pressure sensitive V16P transmitter (16 mm diameter, 74 mm length, 14 g in water). The transmitters represented less than 1% of the sharks' body weight and battery life of the transmitters was approximately 20 days.

The receiver, hydrophone, and laptop computer, along with a non-differential global positioning system (GPS) and depth sounder were installed on a 5.8 m tracking boat. During tracking, the computer automatically downloaded the position (latitude and longitude) directly from the GPS at 5 min intervals. Additionally, bottom depth and GPS position of the tracking boat were manually recorded every 15 min. The tracking software was not available for tracks 1–8 and 11; therefore, the 15 min manually recorded positions were used for analysis. The position of the boat was assumed to be the position of the shark. The range and signal strength of the transmitters varies with model type, depth, turbidity and ambient noise, but generally the boat remained approximately 200–400 m from the shark.

Tracking was continuous; with a crew change every 12 h. Supplies such as fuel, oil, recharged 12-volt batteries (to power telemetry equipment) as well as two trackers were transported in a 4.5 m shuttle boat from the tracking base to the tracking boat. Tracking continued uninterrupted throughout shift changes.

In order to study sharks in different locations within the bay, three tracking stations were established. Lewes, Delaware, provided ready access to the lower southwestern part of the bay. Cape May, New Jersey, provided an opportunity to investigate juvenile sharks residing in the eastern-most section of the bay. The tracking station near Bower's Beach, Delaware, approximately 40 km north along shore from Lewes, enabled tracking of sharks in the northern section of the study area.

Data analysis

Mapping. Manually recorded positions (every 15 min) were used to analyze tracks 1–8 and 11; automatically recorded fixes (every 5 min) were used for tracks 9, 10, 12–25. Tracks were plotted using Geographic Information System (GIS) software by *MapInfo Professional* (MapInfo Corp., Troy, New York) and ArcView GIS (Environmental Systems

Research Institute Inc., Redlands, California). Distance traveled was calculated point to point from 15-min fixes for tracks 1–8, and 11, and from 5-min fixes for tracks 9, 10 and 12–25.

Activity space. Activity space was quantified by using the minimum convex polygon (MCP) method (Odum & Kuenzler 1955). Although researchers suggest modification of the MCP area to prevent overestimation of the area due to landmasses or unusual 'sallies' (Winter 1977, Morrissey & Gruber 1993), it was not deemed necessary to alter the polygons for this study due to the vastness of the bay and lack of landmasses.

Ninety-five percent kernel area, using bivariate normal density kernel (Worton 1989), was also used to estimate the area utilized by individual sharks in the bay. The kernel method uses observation points superimposed by a grid to calculate probability density distributions at each intersection, using information from the entire sample. Observations that are close to a point of evaluation will contribute more to the estimate than will ones that are far from it. Thus, the density estimate will be high in areas with many observations and low in areas with few (Seaman & Powell 1996). Kernel area was obtained using the '*Animal Movement Analysis*' extension (Hooge & Eichenlaub 1997) to *ArcView*, and was used for comparison of activity space calculated with the MCP method.

Home range parameters. To describe shape of activity space an index of eccentricity (ECC) was calculated (referred to as index of linearity in Ables 1969):

$$ECC = L/W$$

where L is the maximum length of the MCP area and W is the maximum width of the MCP area). If $ECC = 1$ the activity space is considered symmetrical. Any $ECC > 1$ indicates the activity space is asymmetrical or increasingly elongate.

To determine if a home range exists for sandbar sharks in Delaware Bay, two site attachment indices were calculated (comparable to Morrissey & Gruber (1993)):

1. Linearity index (LI; Bell & Kramer (1979)):

$$LI = (F_n - F_1)/D$$

where F_n is the last position taken for the shark, F_1 is the first position taken for the shark, and D is the total distance traveled by the shark. A linearity of

1 indicates linear movements without returning to the vicinity (i.e. straight line travel). A LI near zero indicates little movement from the area with a great deal of overlap and reuse of the activity space.

2. Index of reuse (IOR; Morrissey & Gruber (1993) modified from Cooper (1978) and McKibben & Nelson (1986)):

$$IOR = [OV(A_1 + A_2)]/(A_1 + A_2),$$

where $[OV(A_1 + A_2)]$ is the area of overlap between two activity spaces (MCP areas), and $(A_1 + A_2)$ is the total area of both activity spaces. IOR was calculated for individuals tracked continuously for two consecutive days (n = 11) and also included two 47 h tracks. A_1 represents the activity space of the first 24 h and A_2 represents the second 24 h (23 h for two tracks). An IOR of 1 indicates complete overlap of activity space. If IOR = 0 movements are completely isolated, i.e., activity spaces do not overlap.

T-tests were performed to compare LI and IOR for neonates versus juveniles, and tracking location (Delaware versus New Jersey). Comparisons were made between sharks tracked greater than 24 h and again on tracks greater than 47 h.

Rate of movement. Rate of movement over ground was calculated from distance between consecutive 5 or 15-min positions and averaged over every hour for each shark. To examine differences in rates of movement of neonate and juveniles throughout the day, i.e. day, night and crepuscular periods, rates of movement for tracks greater than 24 h (juvenile = 5, neonate = 9) were averaged into six 4-h real-time intervals for a 24 h period (1:00–4:59, 5:00–8:59, 9:00–12:59, 13:00–16:59, 17:00–20:59, 21:00–0:59). A 2 × 6 mixed factorial analysis of variance with repeated measures on the second factor was performed. Because tracking took place throughout the summer, sunset and sunrise differed as much as 1.5 h from June through September. Therefore, all hourly rates of movement during sunrise were encompassed into one 4 h period, and likewise, all hourly rates during sunset were included in another 4 h period. Two 4 h periods included daytime rates of movement and two 4-h periods included nighttime rates of movement.

Water depth. Water depth was recorded from the depth finder every 15 min during several tracks, and compared to a NOAA National Ocean Service estuarine bathymetry map of Delaware Bay. Actual bottom depths were in agreement with the bathymetry estimates, therefore tracks were plotted on the bathymetry map of Delaware Bay, using GIS, to determine water depth for the remaining tracks. T-tests were performed to determine differences in mean water depth for juvenile and neonate sharks and differences in water depth for sharks tracked on opposite sides of the bay (New Jersey vs. Delaware).

Observation-area curve and optimal tracking duration. Observation-area curves were calculated to determine change in activity space over elapsed time. Cumulative MCPs were calculated for every hour of each track and plotted against track time. It is expected that as tracking time increases, or the number of positions increases, activity space will increase initially and eventually reach an asymptote, indicating that area is no longer increasing as tracking time increases. Odum & Kuenzler (1955) suggest that home range be defined at the time when percent change of the observation-area curve is less than 1%. In this study, a less conservative value of 5% recommended by Winter & Ross (1982) was used.

In addition, an exponential decay function was utilized to estimate optimal tracking time. For every track, the percent change in MCP area for each tracking hour was calculated:

$$\% \text{ change} = [(A_t - A_{t-1})/A_t] * 100$$

where A_t is the MCP area at time t, and A_{t-1} is the MCP area at the previous hour, $t - 1$.

Natural logarithms of these percentages for all tracks were linearly regressed against track hour such that the slope, Z, may be used to estimate percent MCP change, P_t, as a function of time:

$$P_t = 100e^{-Zt}$$

The value of t for P_t equal to 5% MCP was accepted as optimal tracking time. This time estimate is specific to juvenile and neonate sandbar sharks in the Delaware Bay study area during the summer.

Results

During the summers of 1998 and 1999, 25 neonate and juvenile sandbar sharks (57–132 cm TL) were tracked for a total of 848 h in Delaware Bay (Table 1). In 1998, 12 sharks were caught and tracked near

Table 1. Summary of juvenile and neonate sandbar sharks tracked in Delaware Bay in 1998 and 1999.

Track	Stage	Sex	Total length (cm)	Weight (kg)	Date	Capture location	Duration (h)	Distance (km)	Rate of movement (km/h)	Polygon area (km²)	95% kernel area (km²)
1	Juv	F	74.0	1.2	24–25 Jun '98	Broadkill	12.3	15.1	1.2	7.1	19.9
2	Juv	M	111.0	9.1	25–26 Jun '98	Primehook	10.0	18.3	1.9	9.6	17.2
3	Neo	F	61.0	1.8	29 Jul '98	Broadkill	6.0	7.3	1.2	2.2	8.0
4	Juv	F	131.0	15.0	30–31 Jul '98	Broadkill	7.3	10.3	1.7	11.9	37.5
5	Juv	M	132.0	na	2–5 Aug '98	Broadkill	70.0	107.5	1.9	36.6	53.1
6	Juv	F	88.0	na	13–15 Aug '98	Broadkill	53.3	59.3	1.3	29.0	39.0
7	Neo	F	61.0	1.7	15–17 Aug '98	Broadkill	48.3	57.9	1.2	13.4	20.2
8	Neo	M	61.0	1.5	18 Aug '98	Mispillion	8.0	10.4	1.3	6.1	19.2
9	Neo	F	59.0	na	21–22 Sep '98	Broadkill	31.0	43.8*	1.4*	6.7	12.5
10	Neo	M	63.0	1.7	16–18 Sep '98	Broadkill	56.0	97.6*	1.8*	110.4	125.8
11	Neo	M	68.0	2.5	18–21 Sep '98	Broadkill	54.0	58.6	1.1	22.9	25.7
12	Neo	F	70.0	na	24–25 Sep '98	Broadkill	24.0	55.9*	2.3*	117.5	163.9
13	Juv	M	124.0	10.8	3–4 Jul '99	Cape May	21.0	40.0*	2.0*	40.5	41.8
14	Juv	M	118.0	10.0	6–9 Jul '99	Town Bank	56.0	118.9*	2.3*	333.9	315.4
15	Neo	F	57.0	1.6	27 Jul '99	Murderkill	2.5	5.7	2.1*	1.1	2.8
16	Neo	M	65.0	na	28–30 Jul '99	Bower's Beach	47.0	70.7*	1.5*	20.8	23.6
17	Neo	F	60.0	na	30–31 Jul '99	Kitts Hummock	32.5	46.3*	1.4*	14.0	15.5
18	Juv	M	103.0	7.0	1–2 Aug '99	Hawk's Nest	17.0	32.6*	2.1*	24.0	40.0
19	Juv	M	117.0	12.0	18–21 Aug '99	Bay Shore Chnl	75.0	122.1*	1.7*	63.7	55.5
20	Neo	M	61.0	1.7	21–23 Aug '99	Deadman Shoal	47.0	74.1*	1.7*	71.9	69.6
21	Neo	M	65.0	2.1	24 Aug '99	Deadman Shoal	5.0	9.8*	1.8*	3.6	4.9
22	Juv	F	115.0	11.3	25–28 Aug '99	Bay Shore Chnl	67.0	139.4*	2.1*	84.6	92.7
23	Neo	M	68.0	2.3	8–9 Sep '99	Primehook	28.5	19.4*	2.2*	96.5	86.4
24	Juv	F	87.0	4.9	10–11 Sep '99	Primehook	17.0	42.8*	2.5*	110.3	94.8
25	Neo	M	60.0	1.5	11–13 Sep '99	Primehook	52.0	98.9*	1.9*	155.2	182.9

Rate of movement and distance traveled were calculated from distance between successive 5(*) or 15 min positions. Tracks 13, 14, 19–22 were in New Jersey water, all others were in Delaware.

Lewes, Delaware adjacent to Broadkill and Primehook Beaches. Thirteen sandbar sharks were tracked during the summer of 1999; six were caught and tracked on the New Jersey side of Delaware Bay near Cape May; four were caught and tracked near Bower's Beach, Delaware; three were caught and tracked off Primehook Beach, Delaware near Lewes (Table 1).

The total distance traveled ranged from 5.7–139.4 km; the duration of the tracks ranged from several hours to several days (2.5–75 h; Table 1). Ten sharks were tracked continuously for up to 24 h;

six sharks were tracked for between 24 and 48 h; eight sharks were tracked for between 48 and 72 h and one shark was tracked for 75 h.

General patterns of short-term movements of sandbar sharks

Juvenile and neonate sandbar sharks primarily occupied coastal areas within Delaware Bay and made occasional excursions across the bay (20+ km, Sharks 12 and 14; Figure 2) or into deeper bay waters (37 m,
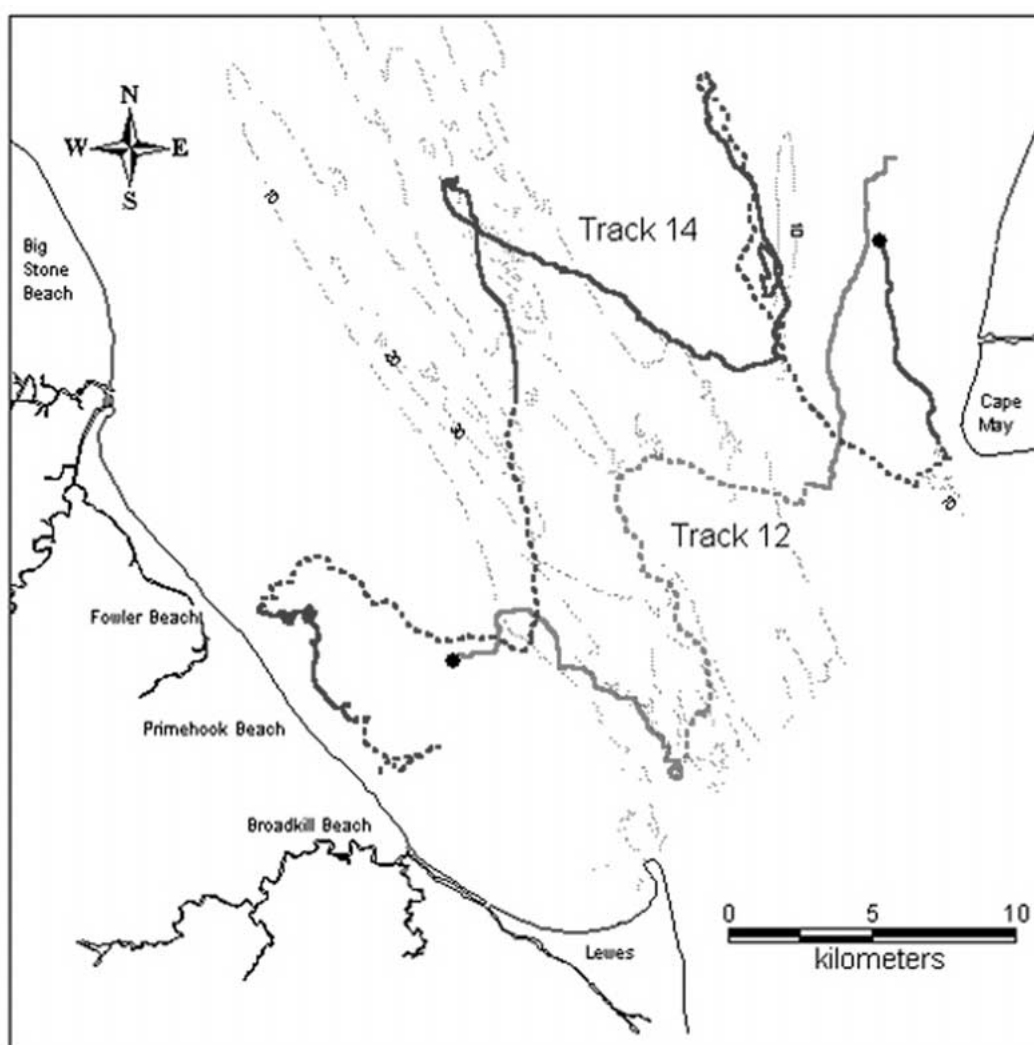
Figure 2. Tracks of sharks that crossed Delaware Bay. Shark 12 (neonate, 70.0 cm TL) was caught in Delaware waters and tracked for 24.0 h between 24–25 September 1998. Shark 14 (juvenile, 118.0 cm TL) was caught in New Jersey waters and tracked for 56.0 h between 6–9 July 1999. Solid line = daytime; dotted line = nighttime; closed circle = start of track.
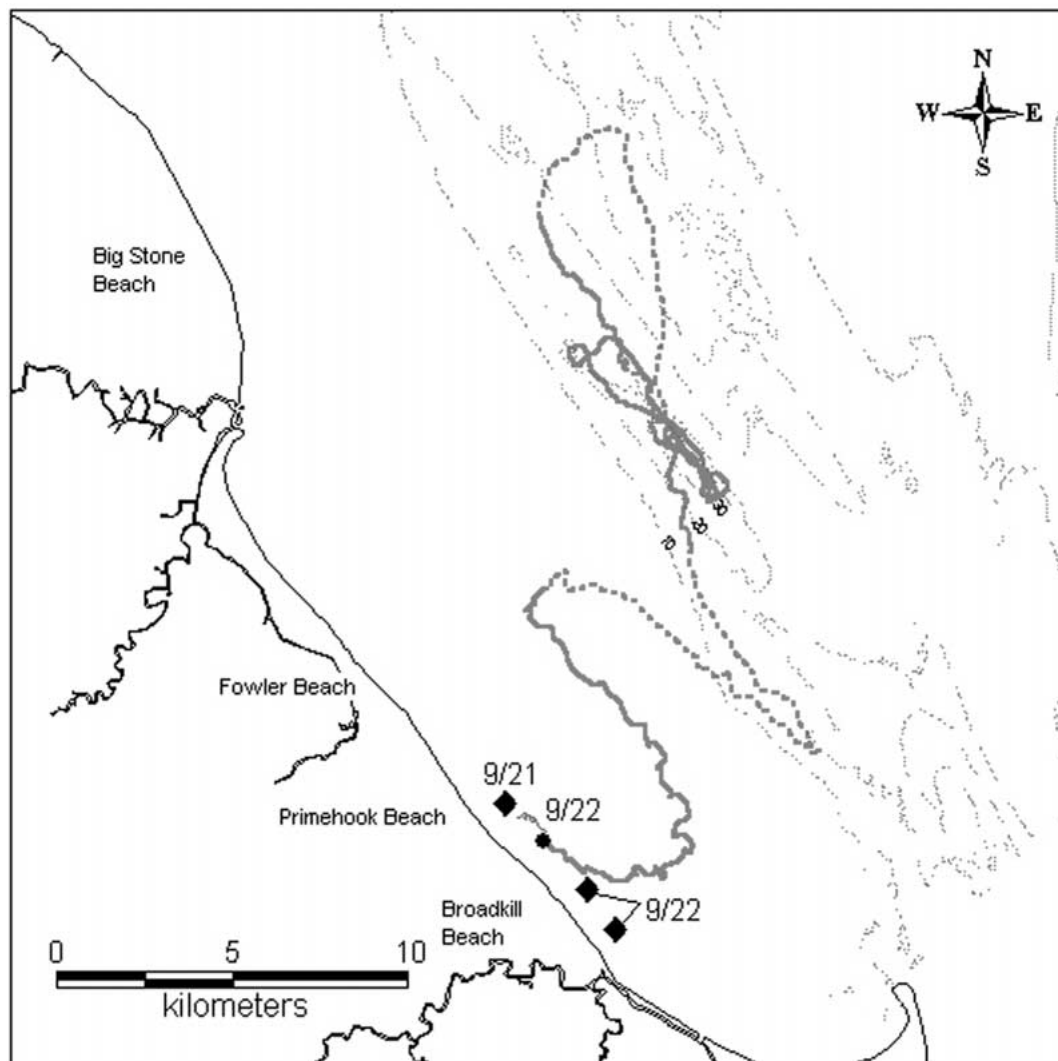
Figure 3. Track of a shark detected multiple times. Shark 10 (neonate, 63.0 cm TL) was tracked for 56.0 h between 16–18 September 1998. Solid line = daytime; dotted line = nighttime. Closed circle = start of track. During a subsequent track (Shark 9, between 21–22 September) Shark 10 was reacquired several times (closed diamonds) and was tracked for a short time (thin solid line northwest of track start) on 22 September.

Shark 10; Figure 3). Sharks caught and tracked on the western side of Delaware Bay generally remained nearshore and in shallow water (Sharks 1–9, 11, 15–18, 25; Sharks 7 and 16 shown in Figure 4). Maximum distance from the Delaware shore (excluding Shark 12 that crossed the bay to the New Jersey side) ranged from 1.8–15.8 km with an average maximum of 5.4 km (n = 18). Sharks caught and tracked on the New Jersey side of the bay roamed farther from the shore and into relatively deeper water (Shark 22; Figure 4). Maximum distance from the New Jersey shore (excluding

Shark 14 that crossed the bay to the Delaware side) ranged from 7.4–21.0 km with an average maximum of 11.5 km (n = 5).

In the Broadkill Beach, Delaware area, sharks frequently came very near to shore, as close as 100 m or less, and into depths as shallow as one meter (Sharks 1, 5–7, 9, 11, 23–25). In contrast, sharks tracked on the New Jersey side seldom ventured nearshore or into extremely shallow water. Sharks in this area occupied the relatively deeper bay shore channel (maximum depth 10 m) that runs parallel to the
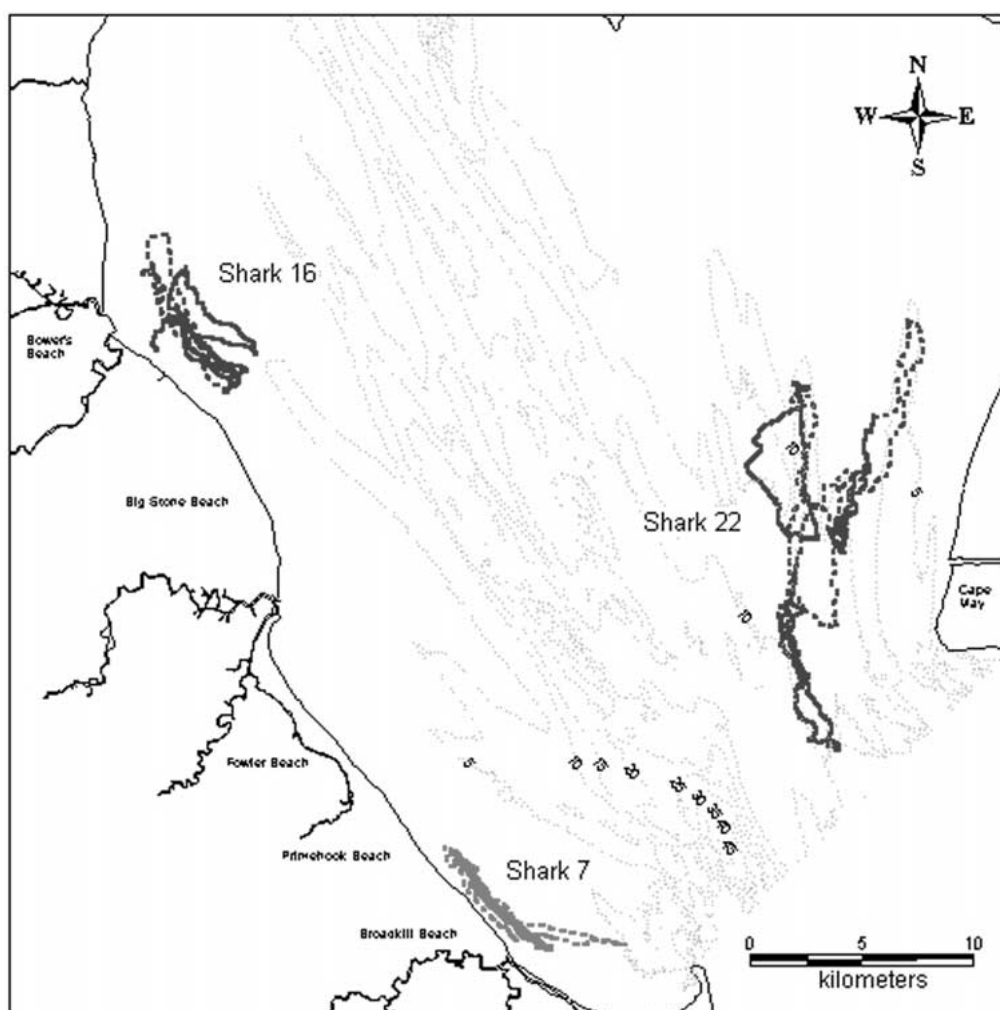
Figure 4. Contrasting behavior typical of sharks tracked on the Delaware side of the bay (near shore/shallow water) and of sharks tracked near New Jersey (farther-afield/deeper-channels). Shark 7 (neonate, 61.0 cm TL) was tracked for 48.3 h between 15–17 August 1998. Shark 16 (neonate, 65.0 cm TL) was tracked for 47.0 h between 28–30 July 1999. Shark 22 (juvenile, 115.0 cm TL) was tracked for 67.0 h between 25–28 August 1999. Solid line represents daytime; dotted line represents nighttime. Closed circle = start location for each track.

Cape May peninsula (Sharks 13, 19, 22). Sharks generally moved northwest to southeast along the Delaware shore and north to south along the New Jersey shore.

Activity space

Activity space, defined by MCP, ranged from 1.0 to 355.1 km^2 (mean = 55.7 km^2; Table 1). The correlation between track duration and activity space was not strong ($r^2 = 0.33$). Longer tracks did not always result in a larger MCP area. Also, there were very low correlations between shark length and MCP area ($r^2 = 0.04$ for all tracks, n = 25; $r^2 = 0.10$ for all tracks over 24 h, n = 15; $r^2 = 0.07$ for all tracks over 47 h, n = 11). Thus, there was no discernible difference for MCP areas of juvenile and neonate sharks.

Although sharks tracked on the New Jersey side of Delaware Bay appeared to occupy a larger activity space than those sharks tracked on the Delaware side of the bay (excluding Sharks 12 and 14, which crossed the bay), there was no significant difference in MCP between tracks for the two sides (New Jersey mean MCP = 52.3, n = 5; Delaware mean MCP = 37.7,

n = 18). Even if all short tracks are excluded, polygon areas for sharks tracked 47 h or greater, which remained on the side of the bay where tracking was initiated, were not significantly different for the New Jersey side (mean MCP = 73.4, n = 3) and the Delaware side (mean MCP = 55.5, n = 7).

Kernel areas for all sharks ranged from 2.82–315.4 km^2 (mean = 62.4 km^2; Table 2). Results from t-tests comparing track area for all sharks (excluding Sharks 12 and 14) tracked in New Jersey (mean kernel area = 52.9, n = 5) and Delaware (mean kernel area = 45.8, n = 18), and for sharks tracked greater than 47 h (New Jersey mean kernel area = 72.6, n = 3; Delaware mean kernel area = 67.2, n = 7), were not significantly different.

Home range parameters

The mean index of ECC was 1.9 (n = 25, range = 1.29–2.75; Table 2), which indicates an activity space where

Table 2. Summary of parameters of home range for 25 sandbar sharks tracked in Delaware Bay.

Shark	Area (km^2)		ECC	Site attachment indices	
	MCP	95% Kernel		LI	IOR
1	7.1	19.9	2.2	0.21	—
2	9.6	17.2	2.0	0.23	—
3	2.2	8.0	2.5	0.48	—
4	11.9	37.5	2.4	0.61	—
5	36.6	53.1	1.8	0.11	0.24
6	29.0	39.0	2.4	0.07	0.25
7	13.4	20.2	2.1	0.06	0.19
8	6.1	19.2	2.8	0.62	—
9	6.7	12.5	2.7	0.06	—
10	110.4	125.8	1.8	0.12	0.00
11	22.9	25.7	1.8	0.06	0.04
12	117.5	163.9	1.6	0.46	—
13	40.5	41.8	1.3	0.11	—
14	333.9	315.4	1.4	0.21	0.00
15	1.1	2.8	2.2	0.51	—
16	20.8	23.6	1.7	0.02	0.38
17	14.0	15.5	1.9	0.15	—
18	24.0	40.0	2.2	0.20	—
19	63.7	55.5	1.3	0.09	0.05
20	71.9	69.6	1.6	0.09	0.19
21	3.6	4.9	1.5	0.30	—
22	84.6	92.7	1.8	0.04	0.08
23	96.5	86.4	1.3	0.23	—
24	110.3	94.8	1.8	0.34	—
25	155.2	182.9	2.2	0.14	0.00
Mean	55.7	62.7	1.9	0.22	0.13

MCP = minumum convex polygon; ECC = eccentricity; LI = linearity index; IOR = index of reuse.

one axis is nearly double the other; therefore, the shape of the activity space for sandbar sharks was generally oval or oblong.

Two site attachment indices were calculated to assess whether juvenile sandbar sharks exhibited site fidelity on their summertime nursery grounds in Delaware Bay. The mean LI was 0.2 (n = 25, range = 0.02–0.62; Table 2). The mean IOR for sharks tracked two consecutive days was 0.1 (n = 11, range = 0–0.38; Table 2). There was no significant difference in site attachment indices for juvenile and neonate sandbar sharks and no significant difference for sharks tracked on the Delaware side of the bay and the New Jersey side of the bay.

Rate of movement

Mean rate of movement over ground for all sharks was 1.53 kmh^{-1} (0.42 ms^{-1}; range = 1.1–2.5 kmh^{-1}). The 2 × 6 mixed factorial analysis of variance for juvenile and neonate shark rate of movement with repeated measures on the second factor (time of day) indicated no significant difference in rate of movement for all sharks between daytime, nighttime and crepuscular periods, and no significant difference in rate of movement between juvenile and neonate sharks.

Depth analysis

Mean bottom depth in areas where sharks were tracked was 5.0 m (mean depth range = 0.96–17.14 m). Sharks spent 72% of the time in waters ≤5 m. Twelve sharks were in water ≤5 m for 100% of the track. There was no significant difference in bottom depth between juveniles (mean = 4.5 ± 2.7 m, n = 5) and neonates (mean = 6.1 ± 6.0 m, n = 10) tracked greater than 24 h. Bottom depth for sharks tracked at different locations within the bay (Delaware mean = 4.7 ± 5.5 m, n = 10; New Jersey mean = 5.3 ± 1.7 m, n = 4) was not significantly different for all tracks greater than 24 h excluding Shark 12 and 14, which crossed the bay.

Observation-area curves and optimal tracking duration

Observation-area curves indicate that many sharks in this study were tracked for a sufficient period of time to accurately describe sandbar shark movements within Delaware Bay (Figure 5). The time in which track area reached an asymptote ranged from 14 h to 56 h. An instantaneous rate coefficient of 0.071 was derived
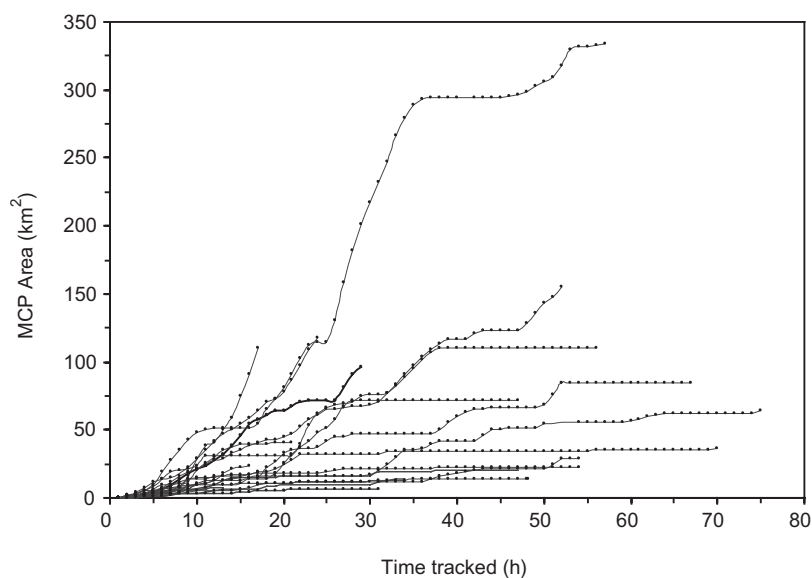
Figure 5. Observation-area curves, determined by MCP area, for 25 sandbar sharks tracked during the summer 1998 and 1999 in Delaware Bay. Area of MCP eventually reaches an asymptote, indicating that activity space increased little with additional tracking time. Total home range area for each shark was estimated based on the time at which MCP area increased less than 5% between consecutive tracking hours.
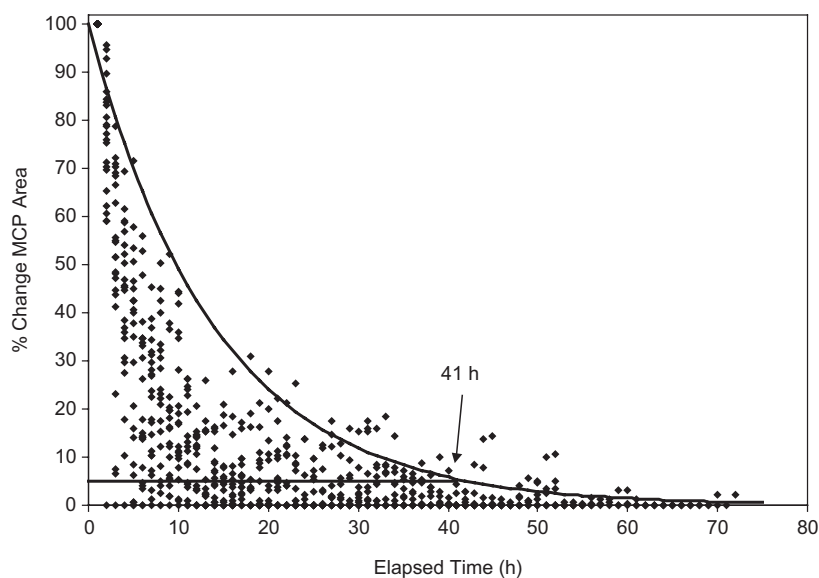

Figure 6. Optimal tracking duration. Exponential decay of percent change of MCP area over time. Curve indicates that the optimal tracking time, based on 5% change, for sandbar sharks in Delaware during summer is approximately 41 h.

from the exponential decay curve fit to the natural log of the percent change MCP (Figure 6). Given the criteria of 5% change, optimal tracking duration is 41 h. This appears to be sufficient time for elucidating typical young sandbar shark behavior using acoustic telemetry during the summer in Delaware Bay.

Discussion

Juvenile and neonate sandbar sharks tracked in our study largely restricted their movements to shallow, near-shore areas in Delaware Bay (Figure 7). Sharks spent 90% of their time in water depth ≤10 m, although
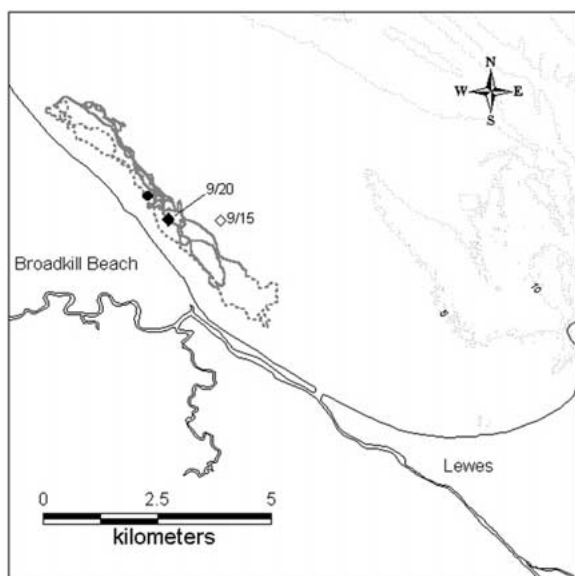
Figure 7. Typical movements of sharks near Delaware. Shark 9 (neonate, 59.0 cm TL) was lost upon initial release on September 15, 1998 (open diamond), but detected during a subsequent track of Shark 11, on 20 September (closed diamond). Shark 9 was reacquired and tracked for 31 h, six days later between 21 and 22 September (closed circle = start of track).

on the eastern side of the bay they generally swam in 5.8–18.2 m deep channels near Cape May. Several sharks crossed the bay entirely, or spent extended periods of time in deep, mid-bay waters. Concentration of sandbar shark activity in shallow water along the shorelines of Delaware Bay observed in our study has also been suggested by extensive gillnet and longline surveys. Merson & Pratt (2001) reported that catch per unit effort (CPUE) in gillnet fishing for sandbar sharks (both neonates and juveniles) in Delaware Bay was highest in the southwestern region, in nearshore waters off the Delaware coast. Wetherbee et al. (2001) reported that longline and gillnet CPUE for sandbar sharks during more recent years were also highest along the western and southeastern coasts of Delaware Bay.

Delaware Bay is considered a shallow bay (Kraft 1991) with extensive shoals along the perimeter of most of the bay and several deep channels (up to 37 m) in the lower middle of the bay. The intense use of this shallow water nursery habitat in Delaware Bay by young sandbar sharks indicated by telemetry and CPUE data is most likely related to predator avoidance, distribution of prey, avoidance of strong mid-bay currents, or a combination of these factors. Relatively, large sand tiger

sharks (*C. taurus*) are found in Delaware Bay during summer, more commonly in deeper portions of the bay (Pratt, pers. comm.). Therefore, young sandbar sharks in shallow waters of Delaware Bay would presumably be less vulnerable to predation by these larger sharks. Stomachs of sandbar sharks caught in the shallow portions of the bay contained several species of crustaceans and fish that are abundant in these regions (Pratt, pers. comm.), and movement patterns of sandbar sharks may reflect distribution of these prey. The importance of nursery areas for providing abundant food sources has been reported in a variety of locations (Springer 1967, Castro 1993).

Relatively strong tidal currents flow through Delaware Bay, particularly in deeper portions of the bay (Rechisky et al., in press). Direction and rate of movement of sandbar sharks in the bay was influenced by direction and speed of tidal currents and movements were independent of time of day. Elevated levels of activity at night have been reported in the majority of studies on movement patterns of elasmobranchs (Sundstrom et al. 2001). In general, the tidal-current-influenced behaviors of sharks on the shallow shelf of western Delaware Bay resembled repetitive, tidally based movements reported for sandbar sharks tracked in Chincoteague Bay, Virginia (Medved & Marshall 1983) and dusky sharks (*C. obscurus*) tracked in the Cape Fear River, North Carolina (Huish & Benedict 1977). However, sandbar sharks tracked on the eastern side of Delaware Bay tended to range farther from shore, cover more ground, occupy deeper water, and show more independence from tidal currents. The movements of these sharks were more comparable to those of sandbar sharks tracked in Chesapeake Bay (Grubbs 2001).

The limited time scale of active tracking methodology precludes quantification of the duration of nearshore site attachment and the frequency of cross-bay excursions. Clearly, the majority of sharks tracked in our study restricted their movements to nearshore waters, but there were exceptions. Obviously, the movement patterns observed for sandbar sharks in the Delaware Bay nursery are only one component of the behaviors of these sharks. In late-September/early-October these sharks leave Delaware Bay and migrate south to winter off the Carolinas and Florida. Two of the three sharks that made cross-bay movements or entered the deep, mid-bay were tracked at the end of the summer. It is possible that increased activity space and long distance movements within Delaware Bay is

common among young sandbar sharks just prior to their departure from the bay.

Activity spaces for sandbar sharks in this study are comparable to those of juvenile sandbar sharks tracked in Chesapeake Bay. In our study, mean activity space for sharks tracked for greater than 40 h was 91.3 km^2 (range: 20.2–355.1 km^2), whereas the mean was 110 km^2 (range: 39.6–275.8 km^2) for sharks tracked over 40 h in Chesapeake Bay (Grubbs 2001). There was no significant difference between size of activity spaces of sharks tracked on the eastern side and the western side of Delaware Bay, however, sharks on the eastern side of the bay behaved similarly to sandbar sharks tracked in Chesapeake Bay, where activity spaces were centered over deeper channels (Grubbs 2001). In Delaware Bay, however, activity space was centered over secondary channels near the coast and not over the deepest mid-bay channels.

The vaiable movement patterns observed in our study enabled a comparison of methods for calculation of activity space: kernel area and MCP area. In general, MCP area was smaller than kernel area for sharks that utilized a core area, and larger for sharks that inhabited large areas, e.g. those that crossed the bay. The difference is greatest at the two extremes. The area occupied by a shark that swam out to the middle of the bay and returned on a different path may be overestimated when using the MCP because it includes interior polygon area not traversed by the shark. The kernel method is not affected by periferal locations (Winter & Ross 1982) and therefore, area estimates may be smaller (and more reasonable) than MCP for extensive tracks. In contrast, individuals with a high percent overlap and that used a relatively confined space generated kernel areas as much as three times greater than MCP. In this case, MCP area may be a more accurate representation of shark movements. Therefore, for our study, MCP may be the best overall estimate of activity space because the majority of sharks tracked remained within a relatively limited area. The elongate shape of activity spaces as determined by the index of ECC is indicative of the near-shore, north–south, patrolling behavior of sharks, with much more limited east–west movements. The predominance of north–south movements appears to be largely a function of reversing tidal currents in Delaware Bay (Rechisky et al. in press).

Home range indices for sandbar sharks tracked in Delaware Bay were also variable, from nomadic to home ranging. Site attachment indices and indices of linearity for sharks tracked throughout at least one complete tidal cycle ranged from extremely repetitive behavior to essentially nomadic behavior. The majority of sandbar sharks revisited areas within Delaware Bay and demonstrated at least some level of home ranging behavior. Sharks tracked in our study had mean LIs similar to those of lemon sharks, which were considered to be site attached in a small lagoon in Bimini, Bahamas (Morrissey & Gruber 1993). However, for sharks in our study that did not revisit the area in which they were tagged, linearity values were as much as one order of magnitude higher than those of lemon sharks in the Bimini lagoon. Indices of reuse for lemon sharks in Bimini were as high as 73% (Morrissey & Gruber 1993), and were much higher than values obtained for sandbar sharks in Delaware Bay. This difference is likely due to the much more restricted area available for lemon sharks within the Bimini lagoon compared to the much larger Delaware Bay.

Sandbar sharks that remained within a core region of Delaware Bay had indices of reuse comparable to those of white sharks tracked in the open-ocean at the South Farallon Islands (Goldman & Anderson 1999). In addition to active tracking data, we obtained ancillary evidence of site attachment of sandbar within Delaware Bay. On five separate occasions we detected sharks that had been tracked previously in the southwestern area of the bay. These detections occurred a week following initial tracks and within 1.5 km from the site where the shark was initially captured. Furthermore, nearly a month following a track, one of our sharks, with the transmitter still attached, was captured by a fisherman in the same vicinity as the shark was originally tracked. Home range indices for sandbar sharks in Delaware Bay are somewhat variable but comparable to home range indices calculated for other elasmobranchs. Many sharks appeared to occupy a home range in the southwestern part of the bay, while others were nomadic. Therefore, sandbar sharks in Delaware Bay would not be strictly classified as home ranging, but rather they have a tendency to inhabit and patrol coastal areas.

Sandbar shark rates of movement in our study were similar to those reported for sandbar sharks (Medved & Marshall 1983) and other charcarhinid species (Huish & Benedict 1977, McKibben & Nelson 1986). Rate of movement of sharks tracked in Delaware Bay did not differ with time of day or size of shark. This finding is somewhat surprising considering the abundance of studies that have reported increased levels of activity at night (Sundstrom et al. 2001), and considering that

juvenile sandbar sharks tracked were as much as 2.3 times larger than neonates. Due to the heavy influence of tidal current on movements of sandbar sharks it is possible that values calculated for speed over ground are more reflective of tidal current than of the shark rate of movement. Rates of movement were calculated based on distance between consecutive positional fixes rather than actual swimming speed of sharks, and were therefore dependent upon the amount of straight-line *versus* meandering swimming between GPS fixes. However, relative rate of movement as calculated in our study are adequate for determination of temporal behavioral changes even if they do not provide accurate swimming speeds of sharks.

Nelson (1990) reported that sharks may have elevated levels of activity for a number of hours following release. Although there was little evidence of post-release-elevated rates of movement of sandbar sharks in our study, several sharks did exhibit behaviors that were possibly associated with the stress of capture and tagging. These sharks made directed eastward movements initially after release, but within several hours had essentially returned to the release site and had begun north–south movements typical of most sharks tracked near the Delaware coast. For all but a few sharks tracked in our study there was little criteria upon which to exclude data from analyses based on aberrant post-release behavior. More detailed studies on physiological changes and recovery occurring following capture and release of sandbar sharks would provide a better indication of the duration of capture-related stress and possible influence on behavior of sharks. In general, sandbar sharks displayed 'typical', patrolling movement patterns very rapidly following release, particularly on the Delaware side of the bay. There was little difference between the initial behavior of most sharks following release and the behavior of one individual that was lost upon release, but was reacquired and tracked five days later. Given the amount of time that had passed between release and reacquisition of this shark, post-release stress from handling was most likely minimal or nonexistent.

Adequate duration of tracks is important for interpreting behavioral information and for extrapolating findings to long-term behavior of a species or population. Because sharks tracked in our study exhibited variable behavior and were tracked for varying lengths of time over varying tidal conditions, we attempted to determine an optimal tracking time for sandbar sharks. We used observation-area curves to derive a theoretical minimum tracking time adequate for characterizing behavior of sandbar sharks in Delaware Bay. The optimal tracking duration of 41 h calculated for sandbar sharks in this study illustrates the importance of continuous tracking for nearly two days to accurately describe behaviors during environmental cycles (i.e. day, night and tidal phases). Many telemetry studies have been conducted on larger and older sharks and it is not unreasonable to presume that some of these species have more complex behaviors than the sandbar sharks studied in Delaware Bay. However, the number of tracks completed and the duration of tracks have not been extensive in a number of these studies. Estimation of optimal tracking time in future elasmobranch studies would provide a useful basis for evaluation of observed behaviors and for increased confidence in the presumption that observed behaviors accurately reflect normal behaviors.

Delaware Bay is an important nursery area for sandbar sharks on the United States East Coast and is a location where management measures that effect a large number of sharks can be enacted to protect or enhance recovery of sandbar shark populations. This study has demonstrated the utility of methodology such as acoustic telemetry for quantifying fine-scale movements of sandbar sharks within a large nursery area. The results of our research have also demonstrated that restricted portions of Delaware Bay are used disproportionately by juvenile sandbar sharks, and thus serve as 'essential habitat'. Management measures designed to curtail overexploitation and efforts to enhance recovery of sandbar shark populations should take into account the importance of areas such as those identified in Delaware Bay and emphasis should be placed on protecting sharks within these areas and on prevention of degradation of this habitat. Future, longer-term monitoring studies aimed at determination of residence times of sandbar sharks within near-shore, shallow areas heavily utilized by sharks in Delaware Bay over extended periods of time, or throughout the entire summer, would further refine understanding of spatial-temporal habitat requirements of these sharks within the bay.

Acknowledgements

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